EXAMINING THE EXISTENCE AND MAINTENANCE OF BEHAVIORAL SYNDROMES IN EASTERN BLUEBIRDS (*SIALIA SIALIS*)

By

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Bachelor of Science in Biology

Indiana University

Bloomington, Indiana

2013

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 2017

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ACKNOWLEDGEMENTS

I would first and foremost would like to thank my adviser Dr. Jennifer L. Grindstaff for mentoring me throughout my time at Oklahoma State University and guiding me through my thesis and Master's career. She was there when I had any question and listened to every idea I had with patience and understanding. She was supportive at every moment and I could not ask for a better adviser. I would also like to thank the members of my committee Dr. Polly Campbell and Dr. Matthew B. Lovern for helping me with my thesis and providing intellectual support. I owe my thanks to other faculty members of the Integrative Biology and Natural Resource and Ecology Management department, such as Dr. Barney Luttbeg for providing assistance with statistical analyses, Dr. Sarah Durant for preparing me for graduate school through her graduate development course, Dr. Karen Mcbee for assisting me with the construction of 3D bird models, Dr. Donald French and Moria Harmon for developing my teaching skills, and Dr. Tim O'Connell for reinvigorating my passion for ornithology and bird watching.

This thesis would not be possible without the numerous undergraduate field volunteers. Particular undergraduate students include Dalton Richardson and Avery Melton for collecting and analyzing data, as well as developing their own independent research projects.

I would like to thank past and present members of the Grindstaff and Durant

Labs: Medhavi Ambardar, Jay Burtka Gatlin, Chris G. Goodchild, Ashley Love, Ann Money, Madeleine Naylor, and Danielle C. Perryman for their continual assistance and support.

My officemates Kelsey A. Deal, Chris G. Goodchild, Miranda L. Kersten, and Danielle C. Perryman have been great friends throughout my time at Oklahoma State and I cannot thank them enough for being there when they were most needed. Their continual support and friendship made it possible for me to excel at Oklahoma State. My most enjoyable memories are with you guys and I will cherish them forever.

I want to thank Susan Weaver, Joanna Mitchell, and numerous teachers at Highland Park Elementary for helping create Science Club in Stillwater, OK. I met Susan randomly while I was doing field work off of HW-51 and her warm, inquisitive personality led to the development of the first afterschool program dedicated to biology and conservation through outdoor activities. Susan and Joanna introduced me to the joys of teaching children biology and ornithology, and I hope to continue this type of program throughout my academic career.

Finally I would like to thank my mom Pallavi Pandit and my sister Caaminee M. Pandit for their inspiration, love, and support. Without them, none of this would have been possible.

Name: MEELYN MAYANK PANDIT

Date of Degree: MAY, 2017

Title of Study: EXAMINING THE EXISTENCE AND MAINTENANCE OF BEHAVIORAL SYNDROMES IN EASTERN BLUEBIRDS (*SIALIA SIALIS*)

Major Field: INTEGRATIVE BIOLOGY

Abstract: Behavioral syndromes are suites of correlated behaviors that can constrain behavioral expression. Constrained behaviors in environments with high levels of human development, which expose individuals to multiple novel contexts, may lead to the expression of suboptimal behaviors that can have fitness implications. Past studies demonstrated that anthropogenic noise can affect vocalizations, but few studies have examined how anthropogenic noise may affect behavioral syndromes. This study examined the existence of behavioral syndromes in eastern bluebirds (*Sialia sialis*) and tested if syndrome strength varied across a gradient of anthropogenic noise. During the breeding season, I conducted multiple behavioral assays on adult bluebirds to measure parental care, aggression, and boldness, respectively. I also recorded anthropogenic noise after each behavioral assay. Males had behavioral syndromes between aggression and boldness and between parental care and boldness, while females had behavioral syndromes between aggression and boldness and between parental care and aggression. High noise habitats slightly weakened the behavioral syndromes in female bluebirds, while anthropogenic noise had no significant impact on male behavioral syndromes. These coupled behaviors may potentially explain the repeatable nest defense aggression behavior in female eastern bluebirds, while selection may favor more plastic aggression in males. Anthropogenic noise may weaken correlated behaviors in female bluebirds, indicating that anthropogenic disturbance may uncouple behavioral syndromes. To determine the full impact of anthropogenic noise on behavioral expression, future studies should examine the effects of experimentally elevated noise levels on individual behavioral phenotypes.

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CHAPTER I

EXAMINING THE EXISTENCE AND MAINTENANCE OF BEHAVIORAL SYNDROMES IN EASTERN BLUEBIRDS

INTRODUCTION

It is often assumed that animal behaviors are plastic to allow animals to adapt to novel situations or changing environments (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004); however, most behaviors have constrained plasticity, which would make these behaviors maladaptive in specific contexts (Sih, Bell, & Johnson, 2004). Some behaviors, such as aggression or parental care, are repeatable, i.e., consistent across different contexts or at different times in many species including invertebrates, reptiles, birds, and mammals (Burtka & Grindstaff, 2013; Dingemanse et al., 2003; Gosling, 2001; Hollander, Van Overveld, Tokka, & Matthysen, 2008). These repeatable behaviors, or personalities, are maintained, even though the behaviors are not adaptive in all contexts. To determine why some behaviors are repeatable across contexts and why there may be limited plasticity, we need to examine individual variation across a suite of behaviors. This will provide insight into how behaviors are related to each other, and therefore, the potential for selection on one behavior to lead to the correlated evolution of related behaviors.

Consistent relationships across behaviors that are maintained over time and across contexts within and among individuals are defined as behavioral syndromes (Sih, Bell, and Johnson, 2004). Relationships between and among behaviors such as parental care, aggression, and boldness have been found in studies of invertebrates (Wilson et al., 2010), reptiles (Stapley & Keogh, 2005), birds (Barnett, Thompson, & Sakaluk, 2012; Gabriel & Black, 2012; Mutzel, Dingemanse, & Kempenaers, 2013), and mammals (Best, Blomberg, & Goldizen, 2015; Rödel et al., 2014) and have demonstrated to affect fitness by limiting the behavioral responses that could be displayed (Smith & Blumstein, 2008). Past research has also demonstrated that intrinsic and extrinsic factors such as body condition (Dosmann, Brooks, & Mateo, 2014; Luttbeg & Sih, 2010; McElreath & Strimling, 2006; Rands et al., 2003) and novel environments (Dingemanse, Dochtermann, & Nakagawa, 2012; Scales, Hyman, & Hughes, 2011), respectively, could affect the maintenance of a behavioral syndrome, indicating that certain behavioral types may be state-dependent. When behaviors such as aggression and boldness are analyzed simultaneously, it is often found that consistent expression of these behaviors may not be optimal across all contexts, but expression is nonetheless repeatable across contexts (Sih, Bell, & Johnson 2004). By analyzing behaviors in tandem, we can understand how they are maintained across time and across contexts, even when this is maladaptive for individuals. By determining if behaviors are correlated with one another, we can understand the limitations of behavioral plasticity. If behavioral syndromes are observed in a population, it is important to understand what effect they have on fitness to determine how they are maintained over time in a population. Ultimately, by identifying factors

such as correlations between behaviors, we can predict how selection is likely to act on coupled behavioral phenotypes over time.

With increasing human development, anthropogenic disturbance is a potential source of selection on behavioral syndromes. This novel type of disturbance may lead to behavioral variation within and among animal populations by exposing individuals to novel situations through habitat change, exposure to pollutants, and introduction of novel organisms (Sih, Ferrari, & Harris, 2011). Anthropogenic disturbance has been demonstrated to selectively favor bolder individuals (Atwell et al., 2012; Scales, Hyman & Huges, 2011). Species and individuals differ in their responses to these novel situations, and if species are unable to shift their average behavioral type to the most optimal behavior, population numbers may decline (Sih, Ferrari, & Harris, 2011; Tuomainen & Candolin, 2011). One consequence of urbanization is an increase in anthropogenic noise. According to the United Nations (2012), human-made noise will continue to increase in the future and spread to remote areas. Most avian vocalizations are high frequency songs, meaning that they can travel over most low frequency noise (Bocharov, Kolesnik, & Soloviev, 2012; Can et al., 2010). Noise from cars and traffic is usually low frequency; however, the amplitude of this noise can be over 65 dB (Barrigon Morillas, Gomez Escobar, Mendez Sierra, Vilchez Gomez, & Trujillo Carmona, 2002; Tsai, Lin, & Chen, 2009; Zannin, Diniz, & Barbosa, 2002), which means that the highest frequency component of this noise can travel far enough to mask bird songs (Brumm, 2014; Nemeth & Brumm, 2010), and can be a potential hazard to birds by changing behavior and increasing stress (Grunst, Rotenberry, & Grunst, 2014; Ríos-Chelén, Quirós-Guerrero, Gil, & Macías Garcia, 2013).

Extensive research has been conducted on the effects of anthropogenic noise on avian signaling behavior, (Catchpole & Slater, 2008), and the strategies birds use to prevent signal degradation (Fuller, Warren, & Gaston, 2007; Lowry, Lill, & Wong, 2012; Nemeth & Brumm, 2009; Proppe, Sturdy, & St. Clair, 2011; Ríos-Chelén, Quirós-Guerrero, Gil, & Macías Garcia, 2013; Slabbekoorn & den Boer-Visser, 2006); however, little research has been conducted on the effects of anthropogenic noise on behaviors such as parental care, aggression, and boldness. A study on urban and rural song sparrows (*Melospiza melodia*) demonstrated that while urban song sparrows are bolder and more aggressive, the correlation between these two behaviors is absent in rural song sparrows (Scales, Hyman, & Huges, 2011). Additional studies are needed to understand how human development, and specific parameters of human development such as anthropogenic noise, could affect the strength of behavioral syndromes. To create effective conservation strategies for at risk species, we need to understand how coupled behaviors change in the increasing number of habitats with disturbance from anthropogenic noise.

Consistent behavioral expression over time and across contexts may be caused by behavioral syndromes because behavioral syndromes constrain behavioral expression (Sih, Bell, & Johnson, 2004). Previous studies have demonstrated that eastern bluebirds (*Sialia sialis*) display consistent parental care and aggressive nest defense behaviors across time and that pair members exhibit coordinated aggressive nest defense behaviors (Burtka & Grindstaff, 2013; Burtka & Grindstaff, 2015). However, neither baseline androgen nor corticosterone levels were related to parental care or nest defense (Burtka, Lovern, & Grindstaff, 2016) and gonadotropin-releasing hormone (GnRH) induced

testosterone levels also were not related to aggression or parental care, indicating that other mechanisms regulate these behaviors (Ambardar & Grindstaff, 2017). Past studies have also demonstrated that anthropogenic noise negatively affects eastern bluebird reproductive success and singing behavior (Kight, Saha, & Swaddle, 2012; Kight & Swaddle, 2015); however, these studies did not examine how anthropogenic noise affected behaviors such as parental care, aggression, or boldness.

In this study I analyzed the relationships among aggression, boldness, and parental care behaviors across multiple contexts to determine if eastern bluebirds exhibit behavioral syndromes. Based on previous studies on multiple bird species (e.g., Barnett, Thompson, & Sakaluk, 2012; Mutzel, Dingemanse, & Kempenaers, 2013), I predicted that there would be a positive relationship between eastern bluebird aggression and boldness, signifying a behavioral syndrome between aggression and boldness (Figure 1). Previous studies have found a negative relationship between aggression and parental care because of the positive effects testosterone has on aggressive behavior and the negative effects testosterone has on parental care in birds (Renée A. Duckworth, 2006; Ketterson & Nolan, 1999; Stoehr & Hill, 2000; Tuttle, 2002). However, as described above, past studies on this population of bluebirds in Stillwater, OK have demonstrated that baseline testosterone levels are not related to aggression or parental care behaviors (Burtka, Lovern, & Grindstaff, 2016). I predicted negative relationships between parental care and boldness because of the potential positive relationship between aggression and boldness and the tradeoff between aggression and parental care (Figure 1). Finally, I predicted that anthropogenic noise would increase the strength of the relationship between aggression

and boldness, while weakening any potential relationships between parental care and aggression and parental care and boldness (Figure 2).

METHODOLOGY

Study Site. Eastern bluebirds nest in secondary cavities and/or in human-made nestboxes and compete with conspecifics, as well as other secondary cavity nesters, such as the invasive house sparrow (*Passer domesticus*) for access to nest sites. Established bluebird nestboxes around Stillwater, Payne County, OK (36˚06'56.57"N, 97˚03'35.15"W) were monitored twice a week for nest activity between mid-February and August in 2015 and 2016. Nestboxes were at least 50 m apart and mounted 1.5 m above the ground on wooden fence posts or metal t-posts in open areas. When a complete bluebird nest was found, I checked boxes daily to determine lay date. Nestboxes were then checked ~13 days after the onset of incubation for hatching. I captured female bluebirds during late incubation in the nestbox to individually mark them with a USFWS aluminum band and a unique combination of color bands to identify them later in the field. Males do not incubate, but enter the box to feed young. Therefore, males were caught between 2-5 days post-hatch and were also given a USFWS aluminum band and a unique color band combination. When the adults were first caught, they were measured for mass (g), wing length (mm), tail length (mm), and tarsus length (mm) with an electronic scale, a wing-chord ruler, and calipers, respectively. This level of monitoring and manipulation has not negatively impacted bluebird nest success in previous field seasons (Burtka & Grindstaff, 2015).

Parental care: Quantifying Food Provisioning. To estimate individual variation in parental investment, I videotaped bluebird visits at 64 total nestboxes between 0700-1100

on days 5-7 post-hatch during 2015 and 2016. I used a small, inconspicuous digital camcorder mounted on a tripod at a distance of about 10 m from the nestbox and a Raspberry Pi camera module (Raspberry Pi Foundation, PiNoir Camera) to record behaviors displayed inside the nestbox. Bluebirds engaged in feeding behavior and did not appear to be disturbed by the presence of either camera (personal obs.; Burtka & Grindstaff, 2015). With the video camcorder and the Raspberry Pi camera, I recorded visitation rate, and calculated the total number of visits per nestling per hour and the fecal sac removal rate, or the total number of fecal sacs removed from the nestbox per nestling per hour. Through the Raspberry Pi recordings, I observed that during approximately 95% of the visits to the nestbox, individuals fed the nestlings. Fecal sacs were only removed after feeding nestlings.

Aggression: *House Sparrow Simulated Territorial Intrusions (HOSP STIs)*. I conducted STIs with a live heterospecific competitor, a male house sparrow, as the intruder to elicit aggressive behaviors from male and female bluebirds at 7-9 days post-hatch. I conducted these trials at 65 total nestboxes during the 2015 and 2016 breeding seasons. House sparrows compete with bluebirds for nesting sites, destroy bluebird eggs, and kill adults or nestlings prior to usurping the nest (Gowaty & Plissner, 2015). For these reasons, bluebirds actively defend nestboxes against house sparrows, and I obtained a measure of aggressive nest defense behavior from this STI. I caught male house sparrows at least 1.5 km from each focal bluebird nest. The house sparrow was kept individually in a galvanized wire cage (22.86 cm wide x 22.86 cm deep x 30.48 cm tall), which was secured to the top of the bluebird nestbox. There was enough space in the cage for sparrows to avoid physical contact from the bluebirds. For each trial, I placed a

covered cage on top of the focal nestbox, removed the cover remotely using a string, and observed behaviors with binoculars from 15 m away. I waited until at least one of the pair-bonded bluebirds at the nestbox arrived within 50 m of the nestbox to begin the observation period and to remove the cover from the house sparrow cage. The trial lasted for two minutes to minimize the amount of stress experienced by the bluebirds and house sparrows. If only one bluebird of the pair appeared during the trial, I continued the trial and scored the behaviors for the bluebird that was present for the trial (during approximately 5% of the trials one bluebird appeared). I recorded the number of times adult bluebirds hovered near the cage, landed on the cage, and attempted to attack the caged house sparrow (Burtka & Grindstaff, 2013, 2015; Duckworth, 2006). I calculated an aggregate aggression score based on the number of these aggressive displays (Table 1).

Boldness: Measuring Responses to Novel Objects. To measure eastern bluebird boldness, specifically neophobia, I conducted novel object trials on nestboxes with nestlings that were 10-13 days post-hatch. At least two trials were conducted: the control trial involved the observer approaching the nestbox, disturbing the nestbox by opening it, and then retreating to an observation base within 20-25 m from the nestbox. I recorded if, and when, the adult male and female bluebird entered established zones (20 m, 5 m, 0.5 m, and entrance to the nestbox), which were used as a measure of distance from the nestbox (Table 2). If neither the male nor the female entered the box after 30 min, the trial ended and I recorded the closest zone each bird entered during the trial. If during the trial the birds entered an established zone, left the territory, and then re-entered the same established zone again, this second zone entrance was not recorded because I was only

interested in the closest zone the bluebird entered. If the birds entered an established zone, left the territory, and then entered a zone closer to the nestbox, this new entrance was recorded. The control trial was conducted to determine if the presence of the observer affected bluebird behavior, and the novel object trial was conducted to determine if the presence of the observer and a novel object affected bluebird behavior. The novel object trial was conducted when nestlings were between 11-13 days old, with a tennis ball as the novel object. I placed the novel object on top of the nestbox, disturbed the nestbox by opening it, and retreated to 20-25m from the nestbox. I then recorded the zones each bluebird entered within the 30 min trial and assigned each bluebird a boldness score for both the control and novel object trials (Table 2). On 20 boxes, I conducted two novel object trials to determine if the boldness behavior was repeatable.

Anthropogenic disturbance measurements. Ambient noise was recorded with a Sennheiser MKE 600 shotgun microphone (Wedemark, Germany) and an H2Next Zoom digital audio recorder (Chiyoda-ku, Tokyo) (Kight, Saha, & Swaddle, 2012; Kight & Swaddle, 2015). I recorded the ambient noise in each cardinal direction for 1 min after the behavioral assays within 10m of each nestbox at which I conducted a behavioral assay. These recordings were calibrated with a Dr. Meter MS10 sound pressure meter during January and February 2017 by recording noise with both the shotgun microphone and sound pressure meter within 10 m of each nestbox at which behavioral assays had been conducted. Audio recordings were analyzed with Audacity 3.0 (The Audacity Team, Pittsburgh, PA). I manually obtained the peak frequency power (dBFS) of 0.5 s sound segments every 10 s for each cardinal direction. Using the "stats" plugin, I obtained the root mean square or RMS amplitude, which is a measure of noise volume magnitude over

time, for 0.5 s segments every 10 s for each cardinal direction. With the calibrated sound pressure meter recordings, I used the predict function in R to determine the sound pressure meter levels (dB) based on the peak frequency power from the recordings conducted during the field season. As a secondary measure of anthropogenic disturbance, I also measured the distance between the nearest road and each nestbox using ArcGIS® v.10.2 (ESRI, Redlands,CA). Past studies demonstrated birds closer to roads had lower reproductive success (Dietz, 2006), and that higher human activity levels led to changes in behavioral expression (Bhardwaj, Dale, & Ratcliffe, 2015), making distance between the nearest road and each nestbox a useful metric of anthropogenic disturbance.

Statistical analyses. All analyses were conducted with R v3.2.2 (R Development Core Team, 2008). I used Akaike information criterion (AIC) model comparisons with the bblme package to find the best fitting models among parental care, aggression, and boldness (Bates et al., 2015). The dataset was divided by sex to account for any sex differences in behavioral expression (Fresneau, Kluen, & Brommer, 2014; Krams et al., 2014; Michelangeli, Chapple, & Wong, 2016). Preliminary analyses included body measurements (wing, tail, tarsus, and mass) in the models; however, none of these measurements were included in the highest fitting models. As a consequence, I included individuals both with and without morphometric measurements in the final model comparisons. Co-factors included in these analyses were the Julian date the behavioral assay was conducted on, pair-bonded partner's behaviors, and brood size. The individual identity number was included as a random effect to account for repeated measures of the same individual. Julian date was scaled by subtracting the mean from each value and dividing the value by the standard deviation to improve model convergence (referred to

as “scaled trial date”). The HOSP STI aggregate aggression score was treated as a ranked ordinal response variable for analyses of the relationship between aggression and boldness and the analyses of the relationship between aggression and parental care. Past studies have used the aggregate aggression score as a continuous variable due to its normal distribution (Burtka & Grindstaff, 2013, 2015). However, the aggregate aggression score was not normally distributed in my dataset, and was thus classified as a ranked, ordinal variable. Consequently, I used cumulative linked mixed models (CLMMs) with the ordinal package in R to analyze the relationship between aggression and boldness (Christensen, 2011). Boldness scores during both the control and novel object trials were used as explanatory variables because they were measures of distance. I then tested which boldness score was most closely related to bluebird aggression by using each boldness score as an explanatory variable in the CLMMs. The control and novel object boldness scores were highly correlated with each other; therefore, the interaction effects between control and novel object scores were excluded from model comparisons. To analyze the relationship between parental care and aggression, cumulative link mixed models were also used, with the HOSP STI aggregate aggression score as the response variable and visitation rate as the explanatory variable. Using the lme4 package (Bates et al., 2015), I conducted linear mixed models (LMMs) to determine the relationships between boldness and parental care, with visitation rate and fecal sac removal rate as the response variables. The sound parameters and the distance to the nearest road (referred to as “road distance”) were scaled for the models to reach convergence. To create one sound parameter, I conducted a principal component analysis (PCA) in R using the scaled power, scaled RMS, scaled predicted sound pressure values, and scaled road distance.

The PCA produced a principal component (PC) with an eigenvalue of 2.430 that explained 60.72% of the variance and which loaded positively for all of the noise measurements (Table 3). This PC was designated as the "noise PC." With this noise PC, I conducted an ANOVA to determine if anthropogenic noise varied across nest box trail sites. A second PC with an eigenvalue of 0.970, explained 24.24% of the variance. Distance to the nearest road loaded positively on this PC and the sound parameters loaded negatively. Since road distance was the only variable that loaded positively in this PC, I used the scaled road distance in the models as another measure of anthropogenic disturbance.

A total of 86 HOSP STIs and 78 parental care trials were conducted during the 2015 and 2016 breeding seasons, and 71 boldness trials were conducted during the 2016 season. Out of these trials, I performed both the HOSP STI and boldness trials at 45 boxes, both the parental care and boldness trials at 65 boxes, and both the parental care and HOSP STI trials at 72 boxes.

I tested a total of 61 individual bluebirds for both aggression and boldness, 52 individuals for both parental care and aggression, and 78 individuals for both boldness and parental care. In a separate set of analyses, I used CLMMs to determine if the noise PC and scaled road distance affected the relationship between boldness and aggression, and if the noise PC and scaled road distance affected the relationship between parental care and aggression. LMMs were used to determine how the noise PC and scaled road distance affected the relationship between parental care and boldness behaviors, with visit rate and fecal sac removal rate as the continuous response variables.

RESULTS

Relationships between boldness and aggression. Nine CLMMs were conducted to analyze the relationship between boldness and aggression scores in females and males (Table 4). For females, the model with the best fit included the control boldness score ($Z = 2.829$, $p = 0.004$) and scaled trial date in the season the trial was conducted ($Z = 2.197$, $p = 0.027$). Aggression scores increased with higher control boldness scores and later scaled trial dates ($Z = -2.629$, $p = 0.008$; Table 5). Aggression scores decreased in bolder females at later scaled trial dates (Figure 3). For the males, the best fitting model included only the control boldness score ($Z = 2.548$, $p = 0.011$; Table 5; Figure 4).

Relationships between parental care and boldness. Seven LMMs were used in the AIC model comparison analysis of relationships between parental care and boldness in females and males (Table 6). The best fitting models for both males and females included the control boldness score and date the trial was conducted (Table 6). However, only in males did the control boldness scores have a significant, negative effect on visitation rate (Table 7). Male visitation rate decreased with the control boldness score ($t = -2.871$, $p = 0.004$), decreased with trial date ($t = -3.851$, $p < 0.001$), and increased in bolder individuals later in the breeding season ($t = 2.598$, $p = 0.003$; Figure 5)

Relationships between aggression and parental care. Seven CLMMs were analyzed with AIC model comparisons for females and males (Table 8). The best fitting model for predicting female aggression included visitation rate (Table 8). Female aggression was significantly higher in individuals with high visitation rates ($Z = 2.511$, $p = 0.012$; Table 9; Figure 6). Males also had a model with visitation rate predicting

aggression (Table 9); however, the relationship between aggression and visitation rate was not significant ($Z = 1.495$, $p = 0.135$).

Trail site anthropogenic noise. Anthropogenic noise varied across the trails sites around Stillwater, OK ($F = 10.343$, $p < 0.001$; Figure 7). The trail with the highest levels of noise PC loading factors was the HW and AS trails, followed by the BG, AG, and PE trails. The trails with the lowest noise PC loading factors were the TR and S5 trails.

Effects of noise on behavioral syndromes. I next examined the relationship between aggression and boldness after including the anthropogenic disturbance explanatory variables (noise PC and road distance) in the models (Table 10). Two models had high fits for females. The best fitting model for females included scaled trial date, the control boldness score, and the noise PC; however, the noise PC did not have a significant effect on the relationship between aggression and boldness in females ($Z = 1.106$, $p = 0.269$; Table 11; Figure 8). The second best fitting model included only the control boldness score and the noise PC, and in this model the noise PC did have a significant, negative effect on aggression scores ($Z = 0.976$, $p = 0.009$) and a significant, positive effect on the relationship between boldness and aggression in females ($Z = 0.233$, $p = 0.018$), indicating bolder individuals in high anthropogenic noise environments had higher aggression scores. For males, three models had high fits: the first model included the control boldness score and the distance to the nearest road; however, scaled road distance did not significantly affect aggression ($Z = 1.309$, $p = 0.190$) or the relationship between aggression and boldness ($Z = -1.383$, $p = 0.167$). The second model included the control boldness score, the novel object boldness score, and the scaled road distance; however, scaled road distance did not affect the relationship between boldness

scores and aggression scores ($Z = -0.880$, $p = 0.379$). The third model included the control boldness score and the noise PC; however, the noise PC did not significantly affect aggression scores ($Z = 0.244$, $p = 0.807$) or the relationship between aggression and boldness ($Z = -0.211$, $p = 0.833$). While the models examining the relationship between parental care and boldness included the scaled road distance (Table 12), this variable did not significantly affect the relationship parental care and boldness in either males or females (Table 13). For the relationship between parental care and aggression, females had one model with high fit (Table 14). The best fitting model included visit rate ($Z = 126042$, $p < 0.001$), the noise PC ($Z = 161462$, $p < 0.001$), and the interaction between visit rate and aggression ($Z = -66257$, $p < 0.001$; Table 15; Figure 9) as the best predictors of female aggression. Males had six high fitting models, but none of the models with anthropogenic disturbance variables had significant effects on the relationship between male aggression and parental care (Table 14).

DISCUSSION

Initially, I predicted that there would be a positive relationship between eastern bluebird aggression and boldness, signifying a behavioral syndrome between aggression and boldness, while there would be negative relationships between these behaviors and parental care (Figure 1). I also predicted that anthropogenic noise would increase the strength of the relationship between boldness and aggression, while weakening the relationships among these behaviors and parental care (Figure 2). Based on my results, there was evidence of a behavioral syndrome between aggression and boldness in both male and female eastern bluebirds, a behavioral syndrome between parental care and boldness in males, and a behavioral syndrome between parental care and aggression in

females (Figures 10A and 10B). When anthropogenic noise was accounted for, only female behavioral syndromes were affected. The behavioral syndrome between aggression and boldness was weaker in females in high noise habitats compared to females in low noise habitats (Figure 11). Anthropogenic noise also negatively affected the behavioral syndrome between parental care and aggression, with females in high noise habitats having a weaker relationship between parental care and aggression than females in low noise habitats. In males, neither the behavioral syndrome between aggression and boldness, nor the behavioral syndrome between parental care and boldness were affected by anthropogenic noise. These correlated behaviors indicate that eastern bluebird behaviors, specifically in females, may be less plastic or flexible than previously thought.

Behavioral syndromes between aggression and boldness have been observed in multiple bird species, so this relationship was also expected to exist in eastern bluebirds (Barnett et al., 2012; Mutzel, Dingemanse, & Kempenaers, 2013; Verbeek, Boon, & Drent, 1996). The relationship between aggression and boldness suggests that more aggressive males and females were more willing to enter the nestbox when a potential threat was on their territory. This behavioral syndrome could also explain why female eastern bluebird nest defense aggressive behaviors are repeatable across time (Burtka & Grindstaff, 2013; Sih, Bell, & Johnson, 2004). If nest defense aggressive behavior is constrained by boldness or by other correlated behaviors, like conspecific aggression, then plasticity in aggressive behavior may be limited. This limitation may prevent individuals from expressing optimal behavior across contexts (Bell, 2005; Duckworth, 2006; Sih, Bell, & Johnson, 2004). Consistent behavioral expression may have long-term

benefits, such as reduced energetic costs associated with limited behavioral plasticity, as shifting behaviors for each context may be energetically costly due to increased sensory inputs and overall neural investment (Changizi, 2003; Iwaniuk, Nelson, & Whishaw, 1999; Westneat & Fox, 2010).

The behavioral syndrome between parental care and boldness in males suggests that bolder males visited the nestbox less for parental provisioning; however, as the breeding season progressed, bolder individuals visited the nestbox more often (Table 7). This shift in direction of the behavioral syndrome may indicate that males invest more energy into parental care as potential breeding opportunities decrease (Trivers, 1972). Another possibility is that our measure of boldness, specifically neophobia, could be another measure of parental care (Beekman & Jordan, 2017). Individuals that enter the nestbox may not be bolder, but instead may be better parents and would enter the nestbox to feed their offspring regardless of a potential predator or a novel object on their territory. Determining what motivates males to enter the box: parental care or boldness, would aid in understanding the behavioral syndrome between parental care and boldness.

The positive relationship between parental care and aggression suggests that there is a behavioral syndrome in females between these two behaviors. This behavioral syndrome represents a female specific behavioral syndrome. The positive relationships between parental care and aggression in bluebirds may signify increased parental investment by females. Females may invest more time and resources into provisioning and nest defense aggression because of the high costs of egg production and incubation. An alternative explanation for this relationship could be that our measure of aggression is an additional measure of parental care because we quantified aggressive nest defense

against a heterospecific cavity competitor. Fresneau and Brommer (2014) used nest defense aggression as a measure of parental care in blue tits (*Cyanistes caeruleus*), and they found that female blue tits had negative correlations between nest defense behaviors and handling aggression in which they held the individual and scored the occurrence of aggressive behavioral displays, while males had positive correlations between nest defense behaviors and handling aggression. However, male nest defense aggression was not related to parental care. In other species, aggression was negatively related to parental care in males (Barnett et al., 2012; Mutzel, Dingemanse, & Kempenaers, 2013). Aggression and parental care may be uncoupled in male bluebirds because males may need to be more plastic in their provisioning rates. A study on pied flycatchers (*Ficedula hypoleuca*) found that males adjust their provisioning rates under harsh food conditions, while female provisioning rates remained consistent across contexts (Mänd, Rasmann, & Mägi, 2013). Male western bluebirds also did not have a significant relationship between parental care and aggression (Duckworth, 2006), indicating that parental care and aggression may be regulated by separate mechanisms in male bluebirds.

At the proximate level, coupled behaviors, such as, aggression and boldness may be regulated by the same hormones (Westneat & Fox, 2010). However, baseline levels of corticosterone and testosterone are not related to parental care behaviors in eastern bluebirds (Burtka et al., 2016). Similarly, eastern bluebird aggression levels are not related to baseline or GnRH induced testosterone levels (Ambardar & Grindstaff, 2017). Furthermore, aggression is not related to baseline androgen levels in western bluebirds, which may mean that organizational effects are more important in establishing consistent aggressive behaviors in bluebirds (Duckworth & Sockman, 2012). Alternatively, the

mechanisms responsible for consistent behavioral expression may be uncovered by testing for relationships with other hormones. For example, levels of the hormone prolactin are associated with parental behavior in some avian species (Buntin, Becker, & Ruzycki, 1991; Vleck, 1998). Visual and tactile stimuli from the nest, eggs, and nestlings stimulate prolactin secretion in birds (El Halawani, Silsby, Behnke, & Fehrer, 1986; Hall, 1987), which switches the parent from sexual activity to parental activity. Eastern bluebird parental care behavior may be regulated by circulating prolactin levels, rather than corticosterone or testosterone levels, which could potentially explain the consistent behavioral expression of parental care in females.

Additionally, multiple mechanisms may affect variation in behavioral syndromes (Sih & Bell, 2008). For example, behaviors related to corticosteroid levels would also be affected by factors that regulate the actions of corticosteroids, like receptor type (i.e., glucocorticoid receptor and mineralocorticoid receptor), receptor densities in different tissues, binding globulin capacity and affinity, and feedback loops with other hormones (Sapolsky, Romero, & Munck, 2000). While studies have focused on the effects of testosterone on aggression, other factors affecting aggression and boldness include vasotocin, vasoactive intestinal polypeptide (VIP), and brain monoamines (Goodson, 1998; Winberg & Nilsson, 1993). Variation in the expression of key genes, such as monoamine oxidase, may also explain the correlation between boldness and aggression (Sih & Bell, 2008). Understanding the complexity behind proximate mechanisms may provide more insight into how behavioral syndromes are regulated.

Although behavioral syndromes may potentially restrict behavioral responses, these relationships are not permanent and can appear for a relatively short amount of time

(Dochtermann & Dingemanse, 2013; Sih, Bell, & Johnson, 2004). Even short-term correlations can impact fitness by causing an individual to display a suboptimal behavior in a disadvantageous circumstance, such as exploratory boldness when predators are present, or when consistent aggressive behaviors are displayed during the nesting cycle (Duckworth, 2006; Sih, Bell, & Johnson, 2004). This raises the question of what are the long-term benefits of these short-term behavioral syndromes, if constrained behaviors could potentially lead to mortality. Dingemanse et al. (2007) demonstrated that three-spined stickleback (*Gasterosteus aculeatus*) behavioral syndromes among aggression, activity, and exploratory behavior only existed in large ponds with predators, while small ponds with no predators had weakened or non-existent relationships, concluding that predation may select for behavioral syndromes as short-term adaptive responses. Coupling behaviors like aggression and boldness would be advantageous in environments with predators because the coupling constrains behavioral expression. Individuals with this behavioral constraint may be unable to express the full extent of boldness and/or aggressive behaviors, preventing the individual from being depredated.

While selection should favor behavioral plasticity for individuals to produce the optimal behavior in any given context, constantly changing behaviors across contexts may lead to costly errors. For example, if an individual mismatches a behavior for a specific context, then this could lead to a high fitness cost and potentially death (Auld, Agrawal, & Relyea, 2010). Behavioral plasticity could also produce behaviors beyond the average phenotypic expression, which may lead to production costs (DeWitt, Sih, & Wilson, 1998). If an individual is able to match its behavior to the environment, but the environment changes rapidly, then the individual may have to invest more into sensory

systems to obtain the correct information from the environment and to match behavior to that specific environment (DeWitt, Sih, & Wilson, 1998). Selection may couple behaviors as a short-term adaptation to reduce the extremes of behavioral expression under certain contexts and to reduce the cost of behavioral plasticity. Behavioral syndromes in female eastern bluebirds may be the result of limiting behavioral expression during the breeding season, which provides multiple different contexts over time. Understanding how behaviors are coupled for a short time frame and the fitness implications of behavioral couplings would be interesting avenues to pursue.

When anthropogenic disturbance was included in the analysis, anthropogenic noise negatively affected aggression scores and weakened the relationship between female aggression and boldness. However, this effect was found in the second best fitting model, which did not include the effects of scaled trial date. This result suggests that while anthropogenic noise may negatively affect the relationship between aggression and boldness, the impact is not as large as other factors, such as date in the breeding season. In a past study on eastern bluebirds in Virginia, Kight, Saha, & Swaddle (2012) found that bluebird pairs in high anthropogenic noise habitats suffered from decreased brood size and productivity (i.e., the number of fledglings that were produced). A possible explanation based on my results could be that females in high noise environments defended their nests less or were less bold in novel situations than females in low noise habitats. Great tits (*Parus major*) also have sex-specific responses to increased ambient noise levels, with bolder females and shier males reducing visit rates during playbacks of disturbing noise (i.e. noise below the great tit vocalization frequency range) (Naguib et

al., 2013). These results suggest that high noise levels may disrupt relationships between behaviors but do not completely uncouple correlated behaviors.

While anthropogenic noise may have a weak effect on the behavioral syndrome between boldness and aggression in females, past studies demonstrated that anthropogenic disturbance affects behavioral syndrome strength. Behavioral syndromes between aggression and boldness that exist in rural populations of song sparrows break down in urban populations (Scales, Hyman, & Hughes, 2011). Behavioral syndromes among food neophobia, risk taking, and activity only existed in rural populations of house sparrows, while urban house sparrows did not have relationships among these behaviors (Bókony, Kulcsár, Tóth, & Liker, 2012). Urbanization produces additional stressors, such as reduced nesting habitat and novel predators. Urbanization provides additional resources such as food, which lead to increases in habituation and boldness behaviors (Atwell et al., 2012; Greggor, Clayton, Fulford, & Thornton, 2016; Scales, Hyman, & Hughes, 2011). Aggression also changes in response to increases in territory quality, as has been shown in Ural owls (*Strix uralensis*), which increase nest defense in territories with more vole prey (Kontiainen et al., 2009). Based on these studies, resource abundance may decouple correlated behaviors. However in my study site, most of the anthropogenic disturbance was generated near roads that did not offer additional resources, and a study on food supplementation did not detect effects on behavioral expression in eastern bluebirds (Perryman, unpublished). To understand how anthropogenic disturbance affects behavioral syndrome strength, further experimental studies on resource abundance in urban environments are needed.

Future research should also examine the direct effects of increased noise on behavioral expression. While this study examined how noise varied across multiple trails, the main measurement of noise was ambient sound, which includes wind and wildlife noise. By examining the direct effects of anthropogenic noise, we can understand how individuals alter their behavior within a short time frame and respond to increased human development. This kind of experiment can be done with a "phantom highway" (Ware, McClure, Carlisle, & Barber, 2015) or by using quantifiable noise playbacks when adults are present (Naguib et al., 2013). Understanding how coupled behaviors are weakened or eventually uncouple may help behavioral ecologists understand selection on integrated behavioral phenotypes. With an increasingly changing world, understanding how human development can affect coupled behaviors, and potentially life history events, may lead to more efficient conservation efforts.

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Table 1. Aggregate aggression scores as determined by the number of hovers and attacks displayed by bluebirds during house sparrow simulated territorial intrusions (HOSP STIs).

Number of Hovers	**Number of Attacks**	**Aggregate Aggression Score**
0	-	1
1-5	-	2
>5	-	3
-	1-5	4
-	6-9	5
-	>9	6

Table 2. Boldness scores as determined by closest approach distance to the nestbox during the control and novel object trials.

Distance from the Box (m)	Boldness Score
>20	1
20	2
5	3
0.5	4
0 (Enters Box)	5

Table 3. Noise loading factors for the "Noise PC." Power refers to the energy of the highest frequency noise (dBFS). "RMS" refers to the root-mean-square amplitude (dBFS) of the noise over a set period of time. The "Predicted Sound Pressure" refers to the sound pressure levels (dB) predicted from a linear mixed model. All sound parameters were scaled by subtracting the value from the mean and dividing the difference by the standard deviation.

Noise Parameter	**PC 1**	**PC 2**	**PC 3**	**PC 4**
Power	-0.617	0.101	-0.324	0.71
RMS	-0.614	0.111	-0.339	-0.703
Predicted Sound Pressure	-0.47	0.03	0.882	-0.01
Road Distance	0.146	0.988	0.045	0.007

Table 4. AICc comparison of the nine CLMM models comparing the effects of boldness on aggression scores in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. "Agg" refers to the ordinal aggregate aggression score, "Trial Date" refers to the scaled house sparrow simulated territorial intrusion (HOSP STI) trial date, and "Control Bold" refers to the control boldness score. I focused on models with a ΔAICc of 0-3, which signifies models with high to moderate fit, respectively.

Sex	**Model**	**AICc**	**ΔAICc**	**df**	**weight**
Females	Agg ~ Trial Date * Control Bold + (1|Indv. ID)	163.5	0.0	6	0.8556
Males	Agg ~ Control Bold + (1|Indv. ID)	160.7	0.0	6	0.9562

Table 5. Coefficient table of the best fitting model for the cumulative link mixed models (CLMMs) examining the relationship between boldness and aggression in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Trial Date” refers to the scaled house sparrow simulated territorial intrusion (HOSP STI) trial date, “Control Bold” refers to the control boldness score. P-values below 0.05 are bolded to represent significant effects on aggression.

Sex	**Coefficients**	**Estimate**	**Std. Error**	**z value**	**p value**
Female	Trial Date	34.658	15.772	2.197	**0.027**
	Control Bold	5.323	1.882	2.829	**0.004**
	Trial Date * Control Bold	-11.475	4.366	-2.629	**0.008**
Male	Control Bold	0.6482	0.2544	2.548	**0.011**

Table 6. AICc comparison of the seven linear mixed models (LMMs) comparing the relationships between boldness and visit rates and boldness and fecal sac removal rates in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Visit Rate” refers to the visit rate (number of visits/nestling/hr), “Fecal Sac Rate” refers to the fecal sac removal rate (number of fecal sacs/nestling/hr), “Control Bold” refers to the control boldness score, “NO Bold” refers to the novel object boldness score, and “Trial Date” refers to the scaled feedwatch trial date. I focused on models with a ΔAICc value of 0-3, which signifies models with high to moderate fit, respectively.

Sex	**Response Var.**	**Model**	**AICc**	**dAIC**	**df**	**weight**
Female	Visit Rate	~ Control Bold * Trial Date + (1|Indv. ID)	134.5	0.0	6	0.459
		~ NO Bold * Trial Date + (1|Indv. ID)	136.3	1.8	6	0.184
		~ 1 + (1|Indv.ID)	136.4	1.9	3	0.177
		~ Control Bold + (1|Indv.ID)	136.8	2.3	4	0.147
	Fecal Sac Rate	~ 1 + (1|Indv. ID)	14.9	0.0	3	0.926
Male	Visit Rate	~ Control Bold * Trial Date + (1|Indv. ID)	128.7	0.0	6	0.950
	Fecal Sac Rate	~ 1 + (1|Indv. ID)	-25.2	0.0	3	0.965

Table 7. Coefficient table of the best fitting models for the linear mixed models (LMMs) examining the relationship between parental care and boldness in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. "Visit Rate" refers to the visit rate (number of visits/nestling/hr), "Fecal Sac Rate" refers to the fecal sac removal rate (number of fecal sacs/nestling/hr), "Control Bold" refers to the control boldness score, "NO Bold" refers to the novel object boldness score, and "Trial Date" refers to the scaled feedwatch trial date. Only coefficient summaries of models that had a higher fit than the null model were displayed here. P-values below 0.05 are bolded to represent significant effects on visit rate.

Sex	**Model**	**Coefficients**	**Estimate**	**Std. Error**	**t value**	**p value**
Females	Visit Rate ~ Control Bold * Trial Date + (1|Indv. ID)	Intercept	2.349	2.601	0.903	0.367
		Control Bold	0.196	0.678	0.289	0.772
		Trial Date	-1.957	4.077	-0.480	0.631
		Control Bold * Trial Date	-0.109	1.088	-0.100	0.921
	Visit Rate ~ NO Bold * Trial Date + (1|Indv. ID)	Intercept	4.483	2.301	1.948	0.051
		NO Bold	-0.353	0.606	-0.583	0.560
		Trial Date	-4.992	3.634	-1.374	0.170
		NO Bold * Trial Date	0.671	1.000	0.685	0.493
Males	Visit Rate ~ Control Bold * Trial Date + (1|Indv. ID)	Intercept	10.083	2.306	4.373	**<0.001**
		Control Bold	-1.595	0.555	-2.871	**0.004**
		Trial Date	-14.027	3.642	-3.851	**<0.001**
		Control Bold * Trial Date	2.655	0.898	2.958	**0.003**

Table 8. AICc summary of the relationship between parental care and aggression in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Agg” refers to the ordinal aggregate aggression score, “Visit Rate” refers to the visit rate (number of visits/nestling/hr), “Fecal Sac Rate” refers to the fecal sac removal rate (number of fecal sacs/nestling/hr), “Part. Visit Rate” refers to partner visit rate, “Part. Fecal Sac Rate” refers to partner fecal sac rate, and “Trial Date” refers to the scaled parental care trial date. I focused on models with a ΔAICc value of 0-3, which signifies models with high to moderate fit, respectively.

Sex	**Model**	**AICc**	**dAIC**	**df**	**weight**
Females	Agg ~ Visit Rate + (1|Indv. ID)	210.7	0.0	8	0.616
Males	Agg ~ Visit Rate + (1|Indv. ID)	170.4	0.0	7	0.298
	Agg ~ 1 + (1|Indv. ID)	170.9	0.4	6	0.242
	Agg ~ Trial Date + (1|Indv. ID)	171.9	1.4	7	0.147
	Agg ~ Part. Visit Rate + (1|Indv. ID)	172.6	2.1	7	0.102
	Agg ~ Fecal Sac Rate + (1|Indv. ID)	172.8	2.4	7	0.090
	Agg ~ Part. Fecal Sac Rate + (1|Indv. ID)	173.3	2.9	7	0.071

Table 9. Coefficient table of the cumulative link mixed models (CLMMs) demonstrating the relationship between visitation rate and aggression in females and males. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Visit Rate” refers to the visitation rate (number of visits/nestlings/hr). All other models, including the null model, with a lower dAIC for males were excluded because these models were not significant. P-values below 0.05 are bolded to represent significant effects on aggression.

Sex	**Coefficients**	**Estimate**	**Std. Error**	**z value**	**p value**
Females	Visit Rate	0.8799	0.3505	2.511	**0.0121**
Males	Visit Rate	0.6604	0.4417	1.495	0.135

Table 10. AICc comparison of the nine cumulative link mixed models (CLMMs) on the relationships between boldness and aggression in males and females with the anthropogenic disturbance variables included. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Agg” refers to the ordinal aggregate aggression score, “Trial Date” refers to the scaled house sparrow simulated territorial intrusion (HOSP STI) trial date, “Control Bold” refers to the control boldness score, “NO Bold” refers to the novel object boldness score, “Brood Size” refers to the brood size, “Noise PC” refers to the principal component containing the anthropogenic noise measurements, and “Road Dist.” refers to the scaled road distance. I focused on models with a ΔAICc value of 0-3, which signifies models with high to moderate fit, respectively.

Sex	**Model**	**AICc**	**ΔAICc**	**df**	**weight**
Females	Agg ~ Trial Date * Control Bold * Noise PC + (1|Indv. ID)	139.4	0.0	10	0.6815
	Agg ~ Control Bold * Brood Size * Noise PC + (1|Indv. ID)	141.8	2.4	6	0.2021
Males	Agg ~ Control Bold * Road Dist. + (1| Indv. ID)	101.2	0.0	6	0.3574
	Agg ~ Control Bold * NO Bold * Road Dist. + (1| Indv. ID)	102.6	1.4	10	0.1776
	Agg ~ Control Bold * Noise PC + (1|Indv. ID)	103.5	2.3	6	0.1122
	Agg ~ 1 + (1|Indv. ID)	103.6	2.4	3	0.1057

Table 11. Coefficient table of the highest fitting models examining the effects of anthropogenic disturbance on the relationship between aggression and boldness in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. "Agg" refers to the ordinal aggregate aggression score, "Trial Date" refers to the scaled house sparrow simulated territorial intrusion (HOSP STI) trial date, "Control Bold" refers to the control boldness score, "NO Bold" refers to the novel object boldness score, "Noise PC" refers to the principal component based on the scaled noise parameters, and "Road Dist." refers to the scaled road distance. P-values below 0.05 are bolded to represent significant effects on aggression. While the null model was the fourth highest fitting model for the males, the coefficient table was excluded here.

Sex	Model	Coefficients	Estimate	Std. Error	z value	p value
Females	Agg ~ Trial Date * Control Bold * Noise PC + (1|Indv. ID)	Trial Date	37.751	27.229	1.386	0.166
		Control Bold	6.457	3.250	1.987	**0.047**
		Noise PC	-7.993	7.894	-1.012	0.311
		Trial Date * Control Bold	-13.256	7.243	-1.830	0.067
		Trial Date * Noise PC	11.427	16.933	0.675	0.500
		Control Bold * Noise PC	2.300	2.079	1.106	0.269
		Trial Date * Control Bold * Noise PC	-3.777	4.432	-0.852	0.394
	Agg ~ Control Bold * Brood Size * Noise PC + (1|Indv. ID)	Control Bold	0.988	0.390	2.533	**0.011**
		Noise PC	-2.554	0.976	0.976	**0.009**
		Control Bold * Noise PC	0.552	0.233	0.233	**0.018**
Males	Agg ~ Control Bold * Road Dist. + (1| Indv. ID)	Control Bold	0.682	0.329	2.073	**0.038**
		Road Dist.	1.674	1.279	1.309	0.190
		Control Bold * Road Dist.	-0.443	0.321	-1.383	0.167
	Agg ~ Control Bold * NO Bold * Road Dist. + (1| Indv. ID)	Control Bold	0.339	0.902	0.376	0.707
		NO Bold	-0.501	1.270	-0.395	0.693
		Road Dist.	-3.429	4.838	-0.709	0.478
		Control Bold * NO Bold	0.181	0.303	0.597	0.550
		Control Bold * Road Dist.	-0.221	1.096	-0.201	0.840
		NO Bold * Road. Dist.	3.189	2.637	1.209	0.227
		Control Bold * NO Bold * Road Dist.	-0.457	0.519	-0.880	0.379
	Agg ~ Control Bold * Noise PC + (1|Indv. ID)	Control Bold	0.673	0.313	2.148	**0.032**
		Noise PC	0.127	0.521	0.244	0.807
		Control Bold * Noise PC	-0.029	0.139	-0.211	0.833

Table 12. AICc comparison of the seven linear mixed models (LMMs) comparing the effects of boldness on visit rates and fecal sac removal rates in males and females with the anthropogenic disturbance variables included. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Agg” refers to the aggregate aggression score, “Visit Rate” refers to the visit rate (number of visits/nestling/hr), “Fecal Sac Rate” refers to the fecal sac removal rate (number of fecal sacs/nestling/hr), “Trial Date” refers to the scaled parental care trial date, “Noise PC” refers to the principal component of anthropogenic noise, and “Road Dist.” refers to the distance to the road from the nestbox. I focused on models with a ΔAICc value of 0-3, which signifies models with high to moderate fit.

Sex	**Model**	**AICc**	**ΔAICc**	**df**	**weight**
Females	Visit Rate ~ 1 + (1|Indv. ID)	123.7	0.0	3	0.962
Males	Visit Rate ~ NO Bold * Trial Date * Road Distance + (1|Indv. ID)	144.4	0.0	10	0.690
	Visit Rate ~ Control Bold * Trial Date * Road Distance + (1|Indv. ID)	146.4	2.0	10	0.248

Table 13. Coefficient table of the highest fitting models examining the effects of anthropogenic disturbance on the relationship between parental care and boldness in males. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Visit Rate” refers to the visit rate (number of visits/nestling/hr), “Fecal Sac Rate” refers to the fecal sac removal rate (number of fecal sacs/nestling/hr), “Trial Date” refers to the scaled parental care trial date, “Noise PC” refers to the principal component of anthropogenic noise, and “Road Dist.” refers to the distance to the road from the nestbox. P-values below 0.05 are bolded to represent significant effects on aggression.

Sex	**Model**	**Coefficients**	**Estimate**	**Std. Error**	**t value**	**p value**
Males	Visit Rate ~ NO Bold * Trial Date * Road Distance + (1|Indv. ID)	Intercept	8.22916	4.369	1.883	0.060
		NO Bold	-1.040	1.100	-0.945	0.345
		Trial Date	-10.070	7.023	-1.434	0.152
		Road Distance	-10.780	6.345	-1.6991	0.089
		NO Bold * Trial Date	1.499	1.783	0.841	0.400
		NO Bold * Road Distance	2.876	1.570	1.832	0.067
		Trial Date * Road Distance	16.501	10.071	1.639	0.101
		NO Bold * Trial Date * Road Distance	-4.464	2.507	-1.781	0.075
	Visit Rate ~ Control Bold * Trial Date * Road Distance + (1|Indv. ID)	Intercept	10.225	4.058	2.519	**0.012**
		Control Bold	-1.436	1.004	-1.430	0.153
		Trial Date	-14.089	6.499	-2.168	**0.030**
		Road Distance	-8.546	7.559	-1.131	0.258
		Control Bold * Trial Date	2.418	1.622	1.490	0.136
		Control Bold * Road Distance	2.276	1.849	1.231	0.218
		Trial Date * Road Distance	12.360	12.170	1.016	0.310
		Control Bold * Trial Date * Road Distance	-3.375	2.976	-1.134	0.257

Table 14. AICc comparison of the seven linear mixed models (LMMs) on the effects of anthropogenic noise on the relationship between parental care and aggression in males and females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Agg” refers to the aggregate aggression score, “Visit Rate” refers to the visit rate (number of visits/nestling/hr), “Fecal Sac Rate” refers to the fecal sac removal rate (number of fecal sacs/nestling/hr), “Trial Date” refers to the scaled house sparrow simulated territorial intrusion (HOSP STI) trial date, “Noise PC” refers to the principal component based on the scaled noise parameters, and “Road Dist.” refers to the scaled road distance. I focused on models with a ΔAICc value of 0-3, which signifies models with high to moderate fit.

Sex	**Model**	**AICc**	**ΔAICc**	**df**	**weight**
Females	Agg ~ Visit Rate * Noise PC + (1|Indv. ID)	123.3	0.0	10	1.00
Males	Agg ~ Trial Date * Road Dist.1 + (1|Indv. ID)	101.7	0.0	5	0.4789
	Agg ~ Trial Date * Road. Dist + (1|Indv. ID)	103.8	2.0	8	0.1721
	Agg ~ Trial Date * Noise PC + (1|Indv. ID)	104.3	2.5	8	0.1350

Table 15. Coefficient table of the highest fitting cumulative link mixed models (CLMMs) for the relationship between aggression and parental care with the anthropogenic noise variables for females. All models included individual identity number (1|Indv. ID) as a random effect to account for repeated measurements. “Agg” refers to the aggregate aggression score, “Visit Rate” refers to the visit rate (number of visits/nestling/hr) and the “Noise PC” refers to the principal component based on the scaled noise parameters.

Sex	**Model**	**Coefficients**	**Estimate**	**Std. Error**	**z value**	**p value**
Females	Agg ~ Visit Rate * Noise PC + (1|Indv. ID)	Visit Rate	0.5130	0.0004	126042	**<0.001**
		Noise PC	0.657	0.0004	161462	**<0.001**
		Visit Rate * Noise PC	-0.270	0.0004	-66257	**<0.001**

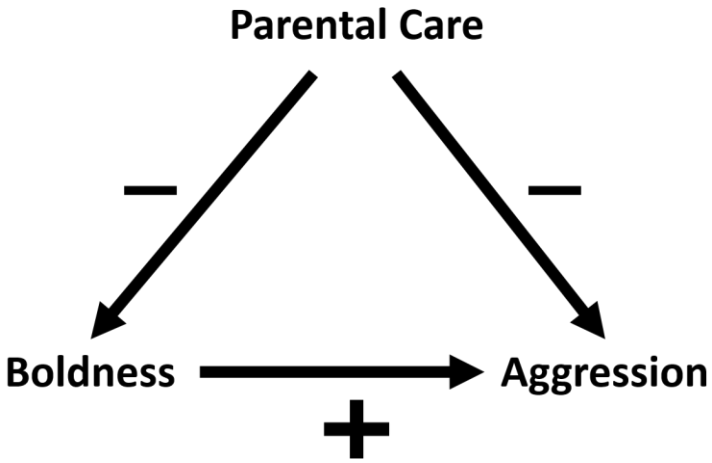


Figure 1. Predictions for behavioral syndromes among parental care, aggression, and boldness in male and female eastern bluebirds. The "+" and "-" signs indicate direction of the relationship, while the thickness of the lines represents the strength of the relationship

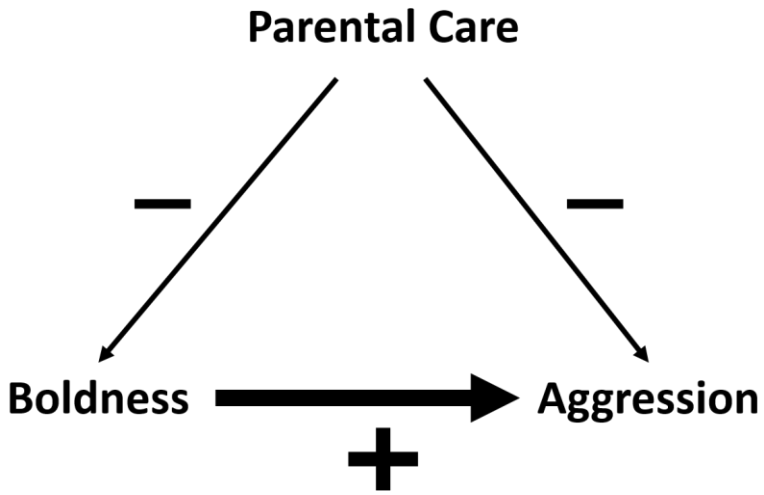


Figure 2. Predictions of the effects of anthropogenic noise on the strength of behavioral syndromes among parental care, aggression, and boldness in male and female eastern bluebirds. The "+" and "-" signs indicate direction of the relationship, while the thickness of the lines represents the strength of the relationship.

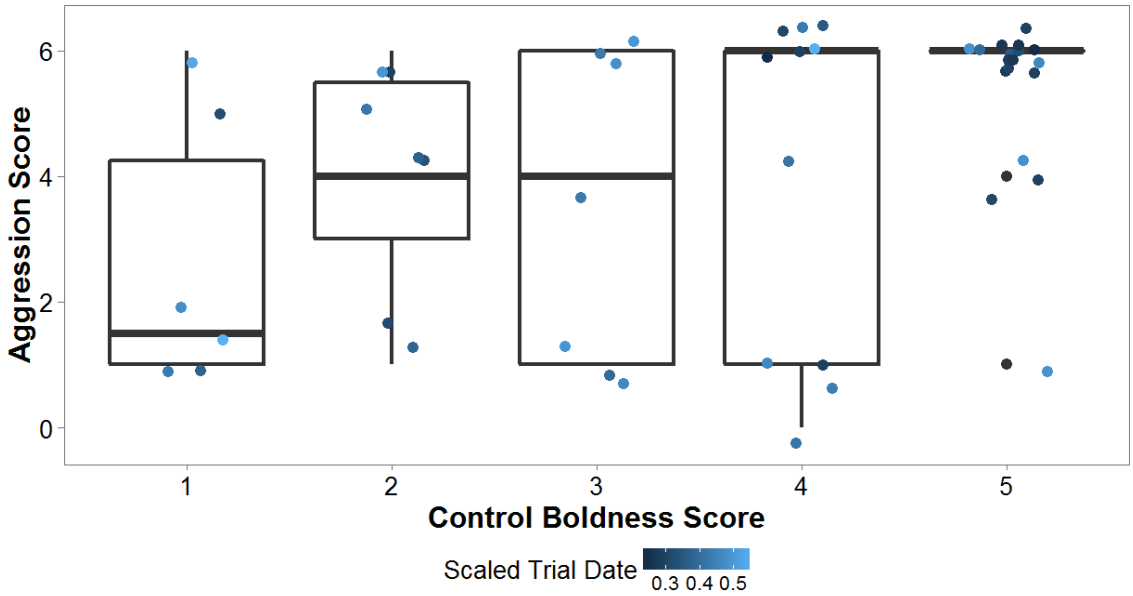


Figure 3. Relationships among female control boldness scores, scaled trial date, and aggression scores (n = 49). A 0.5 jitter was applied to the figure to better illustrate overlapping points. The aggression score refers to the ordinal aggregate aggression score used to categorize bluebird aggression, the scaled trial date refers to the scaled house sparrow simulated territorial intrusion (HOSP STI) trial date, and the control boldness score was a measure of how close the bluebird approached the nestbox during the control novel object trials.

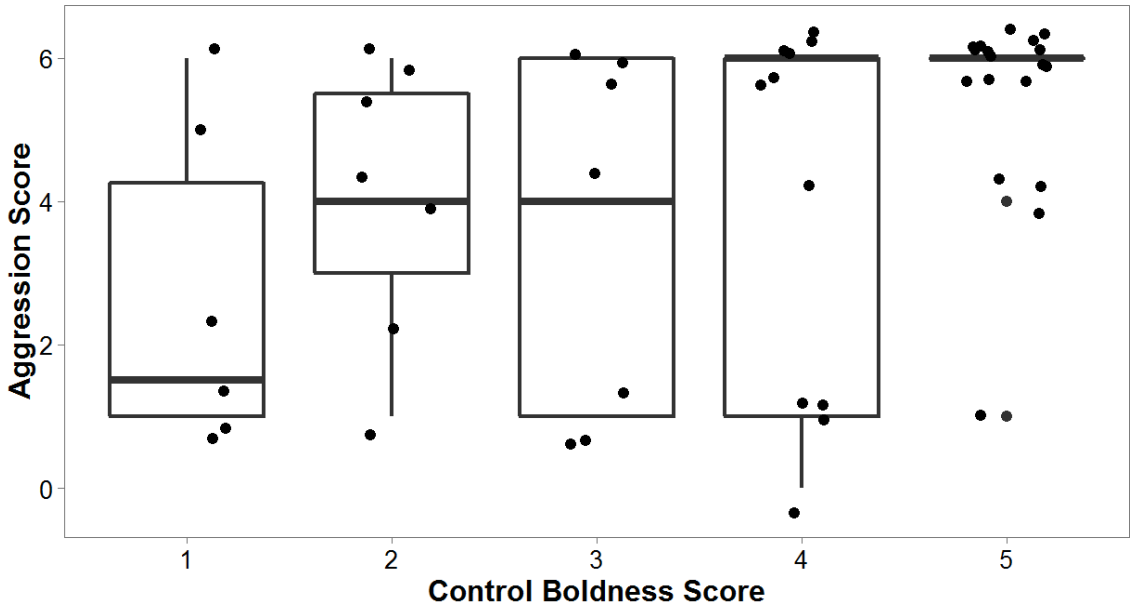


Figure 4. Relationship between male control boldness scores and aggregate aggression scores (n = 49). A 0.5 jitter was applied to the figure to better illustrate overlapping points. The ordinal aggregate aggression score was used to categorize bluebird aggression, and the control boldness score was a measure of how close the bluebird approached the nestbox during the control novel object trials.

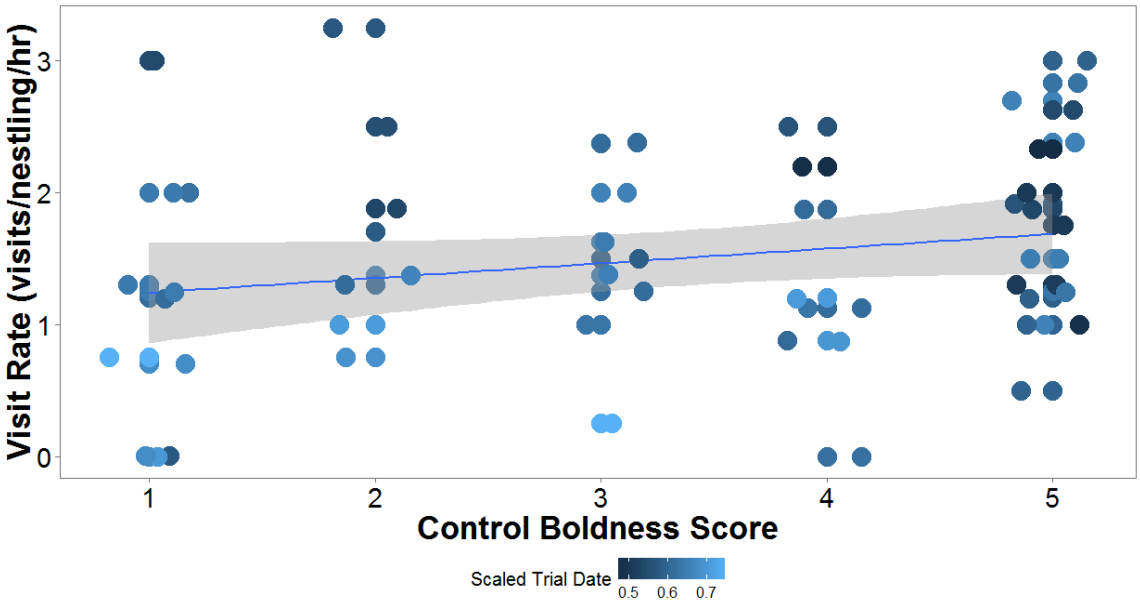


Figure 5. Relationship between male control boldness scores, scaled trial date, and visit rate (n = 56). A 0.5 jitter was applied to the figure to better illustrate overlapping points. The blue line represents the estimate for the interaction between the control boldness score and the scaled trial date, while the adjacent gray area represents the 95% confidence interval. The visit rate was a measure of parental care, the scaled trial date was the date the parental care trial was conducted on, and the control boldness score was a measure of how close the bluebird approached the nestbox during the control novel object trials.

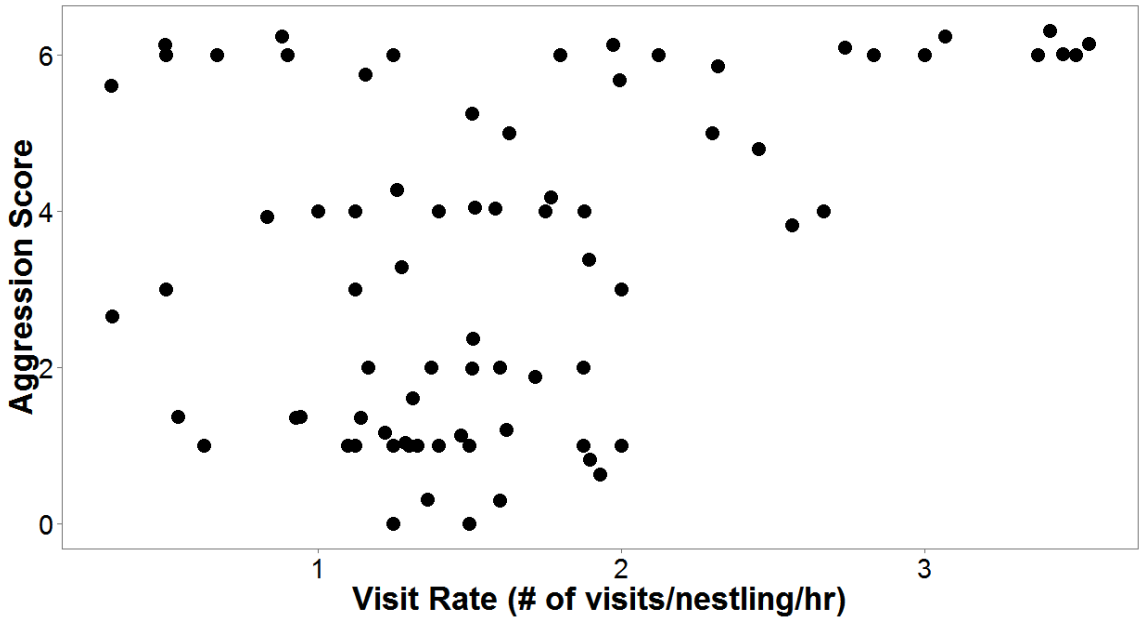


Figure 6. Relationship between female visit rate to the nestbox and aggression scores (n = 57). A 0.5 jitter was applied to the figure to better illustrate overlapping points. The aggression score refers to the ordinal aggregate aggression score used to categorize bluebird aggression and visit rate refers to the number of visits per nestling per hour.

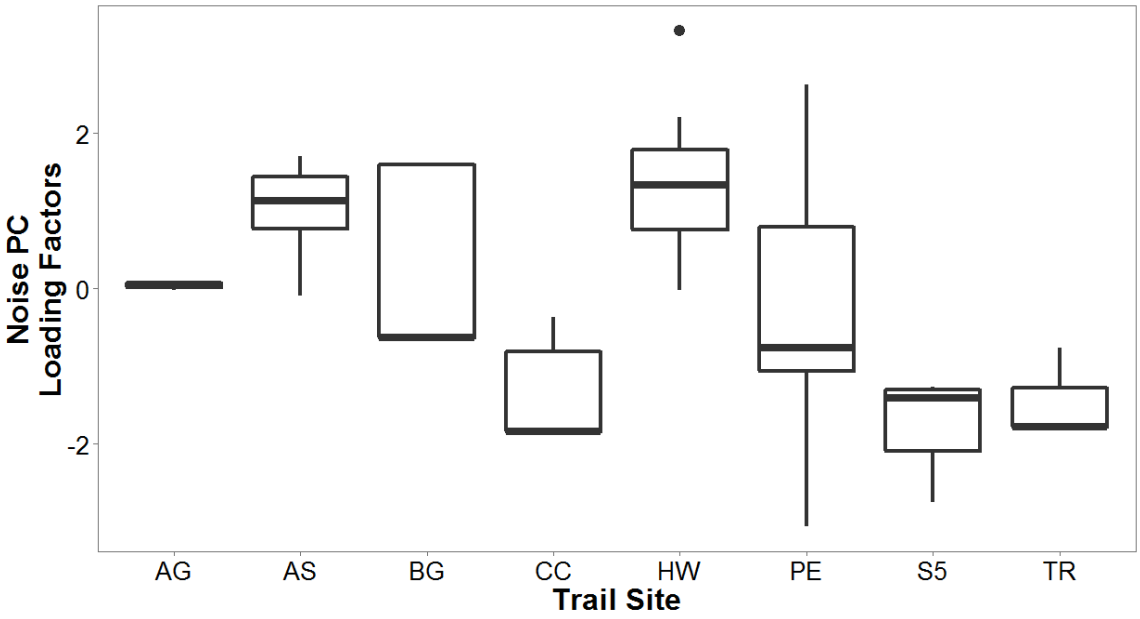


Figure 7. Variation in anthropogenic noise across trail sites. The boxes represent the 1st quartile, the median, and the 3rd quartile, respectively. Lines above and below the boxes represent the minimum and maximum noise PC loading factors for each trail. Black points represent outlier noise PC loading factors.

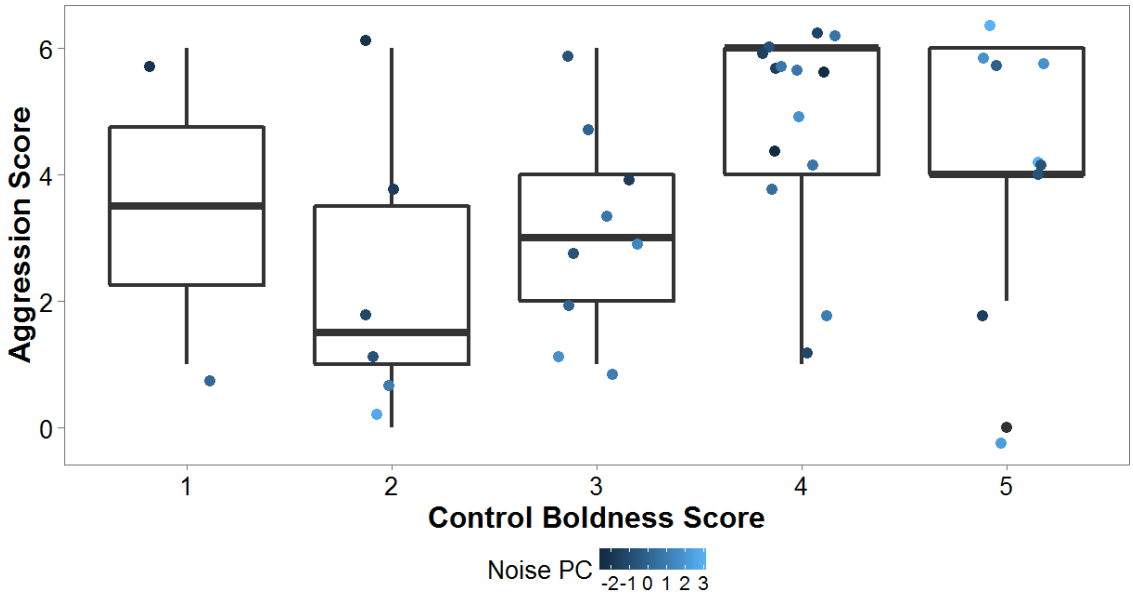


Figure 8. The effects of the noise PC on the relationship between female control boldness scores and ordinal aggregate aggression scores used to categorize bluebird aggression, including the effects of noise (Noise PC; n = 40). The control boldness score was a measure of how close the bluebird approached the nestbox during the control novel object trials. A 0.5 jitter was applied to the figure to show overlapping points. Darker points represent quieter habitats while lighter points represent noisier habitats.

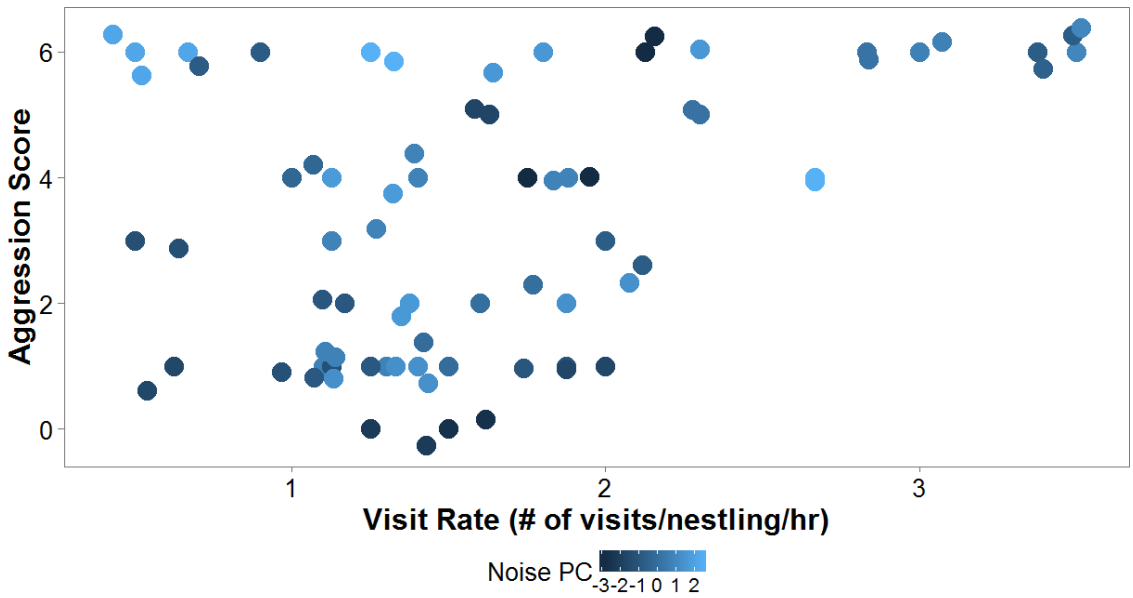
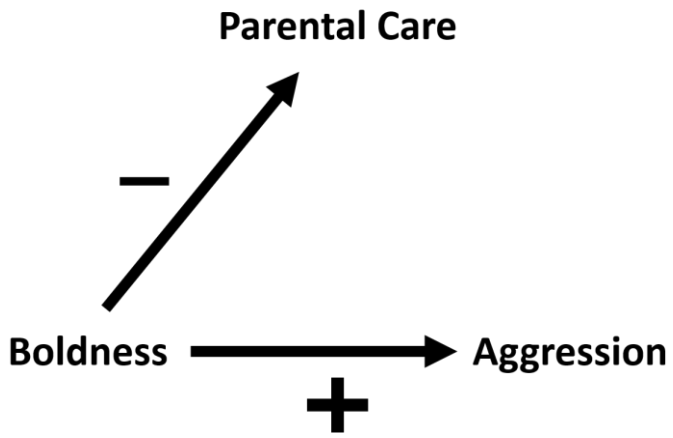
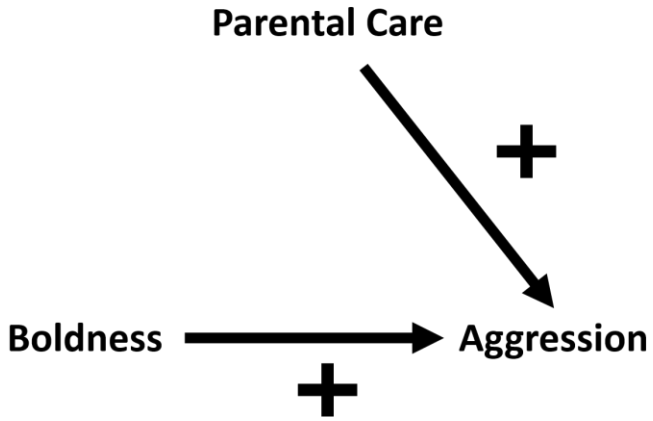


Figure 9. The effects of the noise PC on the relationship between female visit rate and the ordinal aggregate aggression scores used to categorize bluebird aggression (Noise PC; n = 40). A 0.5 jitter was applied to the figure to show overlapping points. The aggression score refers to the ordinal aggregate aggression score used to categorize bluebird aggression and visit rate refers to the number of visits per nestling per hour. Darker points represent quieter habitats while lighter points represent noisier habitats.



10A. Behavioral syndromes found in male eastern bluebirds.



10B. Behavioral syndromes found in female eastern bluebirds.

Figure 10. Behavioral syndromes found in male (A) and female (B) eastern bluebirds. The "+" and "-" signs indicate direction of the relationship, while the thickness of the lines represents the strength of the relationship. Male bluebirds had a positive relationship between aggression and boldness and a negative relationship between parental care and boldness. Female bluebirds had positive relationships between aggression and boldness, as well as parental care and aggression.

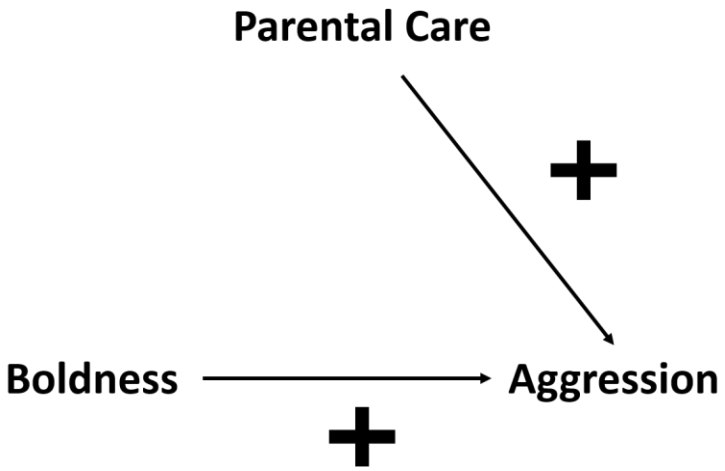


Figure 11. The effects of anthropogenic noise on behavioral syndromes in female eastern bluebirds. The "+" and "-" signs indicate direction of the relationship, while the thickness of the lines represents the strength of the relationship. Anthropogenic noise weakened the relationships between parental care and aggression and between aggression and boldness.

VITA

Meelyn Mayank Pandit

Candidate for the Degree of

Master of Science

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